Metrical and Non-metrical Variation in the Skulls of Gir Lions

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(*With three plates*)

INTRODUCTION

The story of the Indian lion has been told and retold in nearly as many ways as times, but with the exception of the papers by Pocock (1930, 1935), Dharmakumarsinhji & Wynter-Blyth (1951), Wynter-Blyth (1949, 1951, 1956), and Wynter-Blyth & Dharmakumarsinhji (1950) very little of value has been contributed to the topic. Even Pocock's admirable and very useful efforts were greatly hampered by a lack of evidence and material, for when his paper of 1930 was published the fragmentary remains of only a dozen or so Indian lions were available to him throughout the world. Furthermore, only three skulls which he was able to study represented wild-killed animals. This unfortunate situation has been corrected in part by subsequent collection of material and especially by the good fortune of recently obtaining a series of nearly complete skulls and mandibles representing 20 Gir lions. These skulls were ' found ' in November 1963, in a compound adjacent to the Forest Guest House at Sasan Gir. They had been gathered from the Sasan Range of the forest by shikaris over the preceding 5-10 years and allegedly were the remains of animals which had died natural deaths.[1]

Although this paper commences with a comparative study of Gir and African lions, it must be stated at the outset that this comparison is made only to demonstrate features characteristic of Gir lions which may then be studied within the Gir population. Beyond this there are serious theoretical objections attaching to the interpretations of an inter-population comparison. The principal objection revolves around the fact that

[1] Some may have been dispatched by local herdsmen both by poisoning and in at least one instance by what might be reasonably interpreted as a gunshot wound. It was also mentioned by shikaris that some lions had drowned during the monsoon season in 1963. The condition of these specimens is tolerably good in spite of the fact that most of the canine teeth have been removed and the turbinals in most cases are missing. Some of the specimens show the results of having been molested by village dogs, which may also account for the missing mandibles.

the Gir population has been and still is subject to phenomena peculiar to small populations. Ordinarily differences which are found between two populations are attributed directly or indirectly to extrinsic factors on the assumption that both populations approach the classical Hardy-Weinberg model where the effects of inbreeding and chance are insignificant. The Gir population which apparently dwindled to about 25 animals around the turn of the century (Wynter-Blyth 1951) obviously does not conform to this ideal, thereby limiting or invalidating the usual interpretive procedures. A detailed intra-population study is under way, some aspects of which will be discussed below, but the main part of this undertaking will be presented in a future paper.

Methods

As a preliminary to the investigation of the Gir lion skulls, a sample of African skulls[1] was measured in order to generate, albeit somewhat arbitrary, a reference population. This reference population consists of a group of 31 skulls best described as '*P. leo*-African races'. More precisely it is comprised of the individuals indicated in Table I. All

Table I

Subspecific and sex identifications (as per museum notes) of the reference population '*P. leo*-African races'

	Male		Female		?	
P. leo krugeri	8		2		3	
P. leo massaica	2		2		5	
P. leo nyanzae	2		2		1	
P. leo abyssiniae	0		1		0	
P. leo subspp.	2		1		0	
	14	+	8	+	9	=31

captive-born or raised animals, where known or suspected, have been rejected, as these have been shown to be greatly modified by captivity, especially as regards the skull (Hollister 1917). Only those specimens whose sex was recorded and a few which were unmistakably those of males or females because of size and age characteristics have been placed in one or the other category. In the unsexed group there are probably rather more females than males. The only fundamental objection to this group as a reference for the present purpose is that there appears to

[1] Specimens in the collection at the Museum of Comparative Zoology, Harvard University.

have been some preference for large size in assembling the Museum collection. This problem, however, has been taken into account as will be discussed in the analyses reported below. Table II gives the measurements of the sample '*P. leo*-African races' and Table III presents the same measures taken of 16 of the Gir skulls collected in 1963.[1] The measures made are only a portion of those which would ordinarily be employed in a 'classical' study, but they are more than sufficient for the various statistical analyses which have been performed. All measurements have been made to the nearest millimetre.

Discussion and Conclusions

Three analyses of the data from the measurements have been made. All were performed on the IBM 7049 computer, Computation Laboratory, Harvard University. The first, a component analysis[2] serves to indicate principal underlying components in the total variance of the sample and is a measure of redundancy in the measurements taken as a whole. The first principal underlying component explains approximately 95% of the total variance, and represents size almost assuredly as the ranking of individual specimens on this scale reveals. The second component, accounting for about 3% of the total variance, perfectly discriminates between the populations of '*P. leo*-African races' and '*P. leo*-Gir' and, therefore, may be thought of as a measure of 'African-ness' or 'Gir-ness' of these groups. The third component, accounting for about 2% of the variation in these samples, has not been attributed to any particular characteristic, and none of the remaining components clearly relate to sex, a fact which serves to increase confidence in comparisons of the two populations, as there might otherwise be reservations about the differences in sex ratios of the two groups.

The second analysis[3] examines the differences in the means of individual variables between the populations. The variables chosen for this analysis are the ratios of measurements to a standard length (condylobasal length), i.e. a series of indices. This manipulation effectively eliminates size as a variable. In Table IV the means for each variable and the

[1] Measurements were made as follows: (1) Condylobasal length=basal length from anterior end of premaxillary to inferior notch between condyles; (2) Palatal length=length from anterior end of premaxillary to anterior end of posterior nasal opening; (3) Muzzle width=greatest width across muzzle at border of canine alveoli; (4) Intraorbital width=least width between superior border of orbits; (5) Postorbital constriction=least width; (6) Zygomatic width=greatest width across zygomatic arches; (7) Palatal width=width between inner roots of superior carnassials; (8) Mastoid width=greatest width across mastoid processes; (9) Condyle width=greatest width across condyles.

[2] BIMD 02—Component Analysis. BIMD Computer Programs Manual, Division of Biostatistics, School of Medicine, University of California, Los Angeles. 1961.

[3] Bossert, Wm. Analysis of Taxonomic Character Difference. Unpublished Manuscript. Department of Biology, Harvard University.

TABLE II

SKULL MEASUREMENTS OF 'P. *leo*-AFRICAN RACES'

Specimen number	5086	8052	9487	13273	13274	20976	21185	23024	23099	25545	27495	27496	28755	29785	31925	31926
Condylobasal Length	251	282	307	243	291	253	253	291	252	235	282	268	241	312	239	231
Palatal Length	130	146	159	127	156	137	136	155	127	(124)	145	141	132	160	125	120
Muzzle Width	76	91	86	79	92	77	79	89	79	(78)	85	85	(78)	97	74	78
Intraorbital Width	61	69	65	58	64	57	61	69	58	55	65	64	58	72	56	50
Postorbital Constriction	64	60	60	60	57	56	65	63	60	57	58	65	60	62	58	56
Zygomatic Width	212	219	231	187	220	202	207	229	198	184	213	220	181	245	186	173
Palatal Width	71	(80)	(86)	74	78	70	79	84	74	(70)	78	82	67	87	72	68
Mastoid Width	114	133	132	112	134	114	115	136	116	113	135	127	115	138	117	108
Condyle Width	56	67	59	59	71	56	54	67	64	52	61	63	56	68	60	60

Specimen number	31928	36280	36281	36282	36283	36284	36285	37654	37655	37656	37662	37751	37752	37753	46405
Condylobasal Length	231	318	245	282	312	316	315	273	307	319	301	307	311	267	(255)
Palatal Length	124	169	130	155	159	156	162	150	163	167	152	162	163	140	141
Muzzle Width	(75)	97	82	88	90	(95)	90	88	95	96	95	92	95	83	81
Intraorbital Width	45	78	57	69	70	73	74	64	80	74	70	70	74	60	59
Postorbital Constriction	58	70	64	70	62	68	64	63	64	73	68	63	63	61	60
Zygomatic Width	173	249	188	225	236	247	241	208	240	258	238	240	246	196	225
Palatal Width	(69)	86	73	83	81	84	89	82	89	91	81	87	86	75	78
Mastoid Width	111	146	111	130	136	142	137	128	140	147	134	133	140	118	(119)
Condyle Width	63	64	66	65	67	(68)	65	59	64	66	63	65	69	59	(59)

Bracketed figures represent values calculated from regression equation for respective condylobasal length (except specimen 46405 where condylobasal length and other dimensions were calculated from palatal length). A direct determination or reasonable estimate could not be made in these cases due to damage of the specimens. The calculated values were required for the computer programs employed in this study, the alternative being to reject the specimen and those measurements which were directly determined. See text for explanation of measurements.

TABLE III

SKULL MEASUREMENTS OF ' *P. leo*-Gir '

Specimen number	1254	1255	1267	1268	1291	1292	1293	1329	1353	1363	1364	1389	1391	1392	1393	1396
Condylobasal Length ..	262	251	248	249	280	254	239	244	284	260	223	250	235	258	280	282
Palatal Length	130	127	123	124	142	128	121	123	143	127	115	128	118	135	142	141
Muzzle Width	86	82	80	80	91	81	77	77	92	85	73	83	79	86	91	91
Intraorbital Width	64	60	59	65	72	67	57	57	72	62	52	63	59	67	70	71
Postorbital Constriction ..	54	49	51	51	55	53	52	55	58	51	50	51	52	53	52	56
Zygomatic Width	202	195	197	202	232	204	188	197	226	195	(175)	201	190	205	215	235
Palatal Width	76	73	73	75	83	76	70	72	82	74	66	77	72	75	79	82
Mastoid Width	122	115	116	112	132	118	114	117	133	118	104	114	103	118	125	132
Condyle Width	56	53	51	50	56	(53)	51	51	58	57	52	53	46	54	56	56

NOTE. See Table II for explanations

distance (standard deviation) between the two means are presented. As a distance of 2·0 or two standard deviations indicates a significant difference at the 95% level, it can be seen at once that in no single index is there a significant difference. Statistically this means that there is nothing to explain and biologically it implies that the individual differences explain nothing. As a matter of interest, the same procedure was performed to compare independently both of the present lion populations to a series of measurements made on tiger skulls. Again, no significant differences between individual variables were found.

The third analytical procedure employed was a discriminant analysis.[1] Stated simply, this statistical manoeuvre reduces all the indices of all the specimens of the respective populations to two numerical values. These values are, in fact, the means of the distributions of the individual specimens which, similarly, may be represented by single numerical values. For each of the indices a coefficient of discriminant function is generated. This coefficient times the means for each of the indices of the respective populations gives the means of the populations, while the sum of the products of these coefficients times the indices of a given specimen yields a value representing the position of that specimen in the population distribution. According to the relationship of the two distributions to one another, conclusions regarding the significance of difference between the distributions can be made. In this particular case, the distance between the means of the two population distributions exceeds 2·0 standard deviations and there is no overlap between the distributions. The conclusion is, therefore, that in addition to being significantly different at the 95% level, a perfect discrimination can be made for individuals drawn from either of the populations compared on the basis of the measurements taken. Table V shows the distribution given by this analysis while Table IV gives the means, coefficients of discriminant function, products of these, and the per cent contribution to the difference between the population means for the eight products. While these latter calculations cannot be directly equated to the relative importance of the eight variables used in the discrimination, they do fairly draw attention to those which contribute most to the discriminating potential. This in turn stimulates curiosity as to the possible biological significance of the aggregate differences. Referring to Plate I, the regression lines for all measurements *v.* standard length have been plotted. Since the regression line for any two variables passes simultaneously through the means of the two variables, that point defines the mean ratio of the two variables. These mean ratios are, in fact, the indices which are employed in the discriminant analysis. However, it must be remembered that it is the

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[1] BIMD 05—Discriminant analysis-two groups. BIMD Computer Programs Manual, Division of Biostatistics, School of Medicine, University of California, Los Angeles. 1961.

TABLE IV

VALUES EMPLOYED IN ANALYSIS OF TAXONOMIC CHARACTER DIFFERENCE AND DISCRIMINANT ANALYSIS

	MEAN 1 '*P. leo*- African races'	MEAN 2 '*P. leo*- Gir'	Distance (Standard Deviations between the Means)	Coefficient of Discriminant Function (c)	Product Mean 1 × c	Product Mean 2 × c	Per cent Contribution to Difference
Palatal Length	·526	·504	·866	5·9896	3·1505	3·0187	·261
Muzzle Width	·311	·325	·637	−10·3582	−3·2214	−3·3664	·287
Intraorbital Width	·232	·248	·781	0·4016	·0932	·0996	−·012
Postorbital Constriction	·227	·206	·542	4·1771	·9482	·8605	·174
Zygomatic Width	·7835	·795	·322	−0·2655	−·2080	−·2111	·006
Palatal Width	·2866	·294	·289	−5·1509	−1·4767	−1·5144	·075
Mastoid Width	·459	·462	·083	−2·2362	−1·0264	−1·0331	·013
Condyle Width	·227	·208	·682	5·2076	1·1821	1·0832	·196
				Population means	−0·5585	−1·0630	1·000

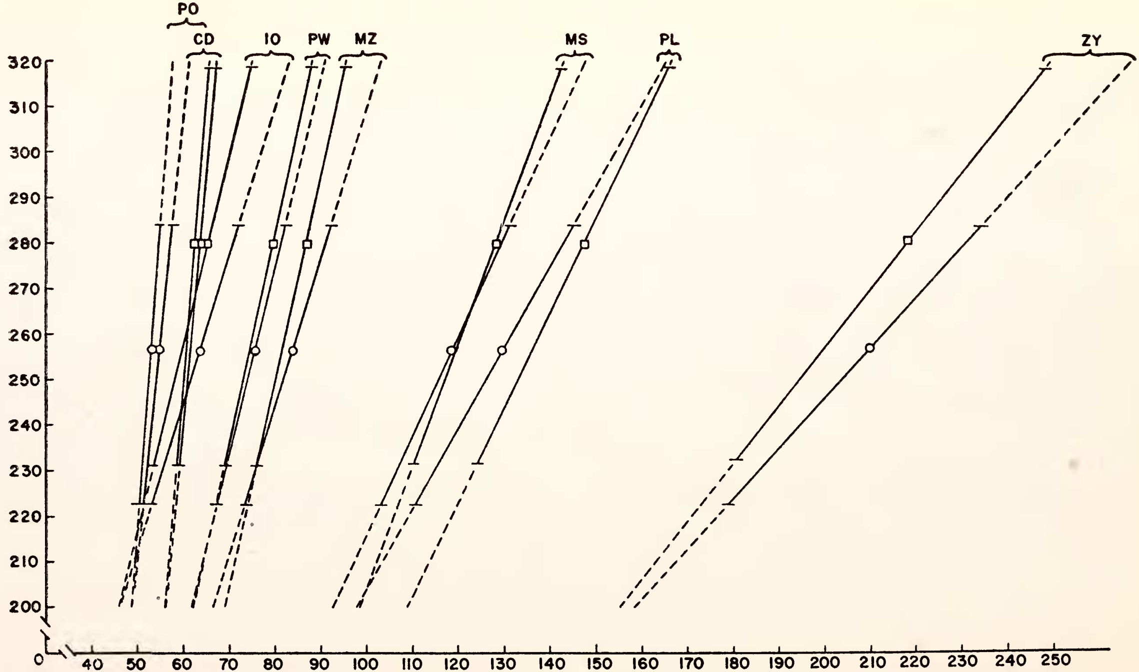
NOTE.—See text for discussion

distributions about these means and not the means themselves nor the regression lines which form the basis of the discrimination between populations. Hence the differences or similarities between any pair of regression lines cannot be taken as implying anything about significance, as shown by the second analysis. Nevertheless, as the aggregate

TABLE V

POPULATION DISTRIBUTIONS GIVEN BY DISCRIMINANT ANALYSIS

Rank	'*P. leo*-African Races'	'*P. leo*-Gir'	
1	−0·3635		
2	−0·3861		
3	−0·4066		
4	−0·4099		
5	−0·4125		
6	−0·4237		
7	−0·4528		
8	−0·4926		
9	−0·4978		
10	−0·5015		
11	−0·5124		
12	−0·5141		
13	−0·5200		
14	−0·5282		
15	−0·5380		
16	−0·5511		
17	−0·5688		
18	−0·5696		
19	−0·5697		
20	−0·5723		
21	−0·5907		
22	−0·6265		
23	−0·6545		
24	−0·6600		
25	−0·6623		
26	−0·6847		
27	−0·6945		
28	−0·7091		
29	−0·7249		
30	−0·7250		
31	−0·7474		
32		−0·8332	(BNHS 1364)
33		−0·9322	(BNHS 1329)
34		−0·9730	(BNHS 1293)
35		−0·9974	(BNHS 1392)
36		−1·014	(BNHS 1292)
37		−1·067	(BNHS 1393)
38		−1·067	(BNHS 1353)
39		−1·071	(BNHS 1255)
40		−1·084	(BNHS 1363)
41		−1·096	(BNHS 1254)
42		−1·112	(BNHS 1268)
43		−1·118	(BNHS 1267)
44		−1·134	(BNHS 1389)
45		−1·149	(BNHS 1396)
46		−1·165	(BNHS 1291)
47		−1·203	(BNHS 1391)



Regression lines of skull measurements *v.* standard length (in mm.) for *P. leo*-Gir (O) and *P. leo*-African races (□)
CD = condyle width; IO = intraorbital width; MS = mastoid width; MZ = muzzle width; PL = palatal length; PW = palatal width; ZY = zygomatic width. **See text for discussion.**

differences are significant it is therefore profitable to look at the nature of the individual differences, especially those which contribute most to the discriminating potential. In comparing the skulls of the two populations a differentiation into a facial and cranial portion or neuraxial and non-neuraxial portion appears. The measurements indicate that the Gir lion tends to be broader but shorter in the facial or non-neuraxial region than the African lion, while in the cranial or neuraxial region this tendency is reversed. In Gir lions, the mastoid dimension shows an interesting pattern when compared to African animals. The smaller (and presumably younger) Gir specimens are relatively narrower in this measurement while larger specimens are relatively broader. It would appear that the mastoid width is determined by a neuraxial influence (brain size) in younger animals but in progressively more mature individuals, a non-neuraxial relationship becomes more pronounced as its development is increasingly influenced by musculature. These observations suggest that the determination of cranial capacities for the two populations might yield interesting results.

With regard to non-metrical and inter- and intra-population studies it is appropriate to consider the following facts at this time. Pocock (1930), in summarizing the differences between Indian and African lion skulls, mentions the flatness of the auditory bullae in the former. Among the present sample this distinction is readily apparent. Pocock's statement, ' but beyond question they [the bullae] are in almost all cases considerably more inflated in African skulls than in the Indian specimens I have seen ', is perfectly applicable to the present groups. A second feature which Pocock found remarkable about the Indian lion was the frequent division of the infraorbital foramen, either unilaterally or bilaterally, into upper and lower openings which were separated by a bridge of bone. In African lions such a situation is unknown. In Tables VI and VII are summarized the condition found in 15 skulls which date from 1822-1931 and in 19 specimens from the 1963 Sasan ' find '. Of the earlier 15 animals, a total of ten show this peculiarity. Whether significant or not, it is interesting to note that this trait was manifested in four out of five skulls recorded for the 19th century, while in ten skulls described between 1910-1931 it is present in six. Finally, among the most recent material, 1953-1963 approximately, a divided foramen is seen in only 5 out of 18½ (as one side of one specimen is missing and one skull is fragmentary) individuals. At the same time as the incidence of affected individuals appears to diminish, the extent of the affection also diminishes. If affected foramina rather than individuals are totalled the differences become much more striking (? and significant), i.e. 1822-1857, 7/10 or 70·0%, 1910-1931, 8/20 or 40·0%, 1953-1963, 6/37 or 16·2%. The temptation is great, even if not justified, to speculate that the condition and its expressivity and/or penetrance are under the influence

TABLE VI

THE CONDITION OF THE INFRAORBITAL FORAMINA IN INDIAN LIONS

	Date	Locality	Museum & No.	Condition of infraorbital foramina Left	Right	Remarks
1	1822	North Gujarat	RCS 4484	Double	Triple	Destroyed in bombing—1941
2	1830	Assund	RCS 4485	Double	Normal	
3	*c.* 1833	?	———	Double	Double	Lost, see Pocock (1930) pp. 653, 657
4	*c.* 1833	?	———	Double	Double	
5	1857	Gir	BM 57.2.24.1	Normal	Normal	Died after *c.* 2 yrs. in captivity
6	*c.* 1910	Amerli	BM 30.6.6.1	Normal	Normal	See Pocock (1930) p. 657
7	*c.* 1910	Amerli	BM 30.6.6.2	Normal	Double	
8	*c.* 1910	Amerli	BM 30.6.6.3	Double	Normal	
9	1920	Gir	CMNH 31121	Double	Double	
10	1929	Gir	AMNH 54995	Normal	Normal	
11	1929	Gir	AMNH 54996	Double	Double	
12	1930	Gir	BNHS 5745	?	?	See Pocock (1930) ed. note p. 665 specimen of Col. Mosse—cannot trace
13	1930	Gir	———	Normal	Double	See Pocock (1930) p. 665 specimens of H. H. the Maharajah of Nawanagar—cannot trace
14	1930	Gir	———	Normal	Double	
15	1931	Gir	BNHS M5744	Normal	Normal	Shot by H.H. the Nawab of Junagadh see Pocock (1930) ed. note p. 665
16	*c.* 1931	Gir	BNHS M5926	Normal	Normal	Specimen presented to the Society by Col. Burton

NOTE.—AMNH—American Museum of Natural History; BNHS—Bombay Natural History Society; RCS—Royal College of Surgeons; BM—British Museum; CMNH—Chicago Museum Natural History.

of only a few polygenes which have shown considerable shifts in frequency over the past 140 years, possibly due to genetic drift. The pivot point or bottleneck for population size is around the turn of the century when

TABLE VII

THE CONDITION OF THE INFRAORBITAL FORAMINA IN LIONS OF THE 1963 GIR 'FIND'

	Date	Locality	Museum & No.	Condition of infra-orbital foramina Left	Condition of infra-orbital foramina Right	Remarks
1	1953-1963	Gir	BNHS 1254	Normal	Double	
2			BNHS 1255	Normal	Normal	
3			BNHS 1261	Normal	———	Right side broken away
4			BNHS 1267	Normal	Normal	
5			BNHS 1268	Normal	Normal	
6			BNHS 1291	Normal	Normal	
7			BNHS 1292	Double	Normal	
8			BNHS 1293	Normal	Normal	
9			BNHS 1329	Normal	Double	
10			BNHS 1353	Normal	Normal	
11			BNHS 1363	Normal	Normal	
12			BNHS 1364	Normal	Normal	
13			BNHS 1389	Normal	Normal	
14			BNHS 1391	Normal	Double	
15			BNHS 1392	Normal	Normal	
16			BNHS 1393	Normal	Normal	
17			BNHS 1396	Normal	Normal	
18			BNHS ——	Double	Double	Number not available
19			BNHS ——	Normal	Normal	Number not available
20			BNHS ——	———	———	A very broken skull, no number assigned

the number of animals dwindled to about 25 and the effective breeding population might have been as low as half a dozen animals. Seven additional skulls not recorded in Table VI are in the collection of the British Museum. While dates of death are not ascertainable for most of these, six represent a time span from April 1865 to 1 January 1945. Among these six there are six divided and six normal foramina. This frequency of 50% is identical to the cumulative frequency for the 15 animals noted in Table VI for the time span 1822-1931. The seventh specimen which died in 1951 or 1952 has both infraorbital foramina normal. As the intra-population studies are pursued, both through extracting data from older material and through the collection on new material, these considerations will hopefully be clarified.

An additional feature characteristic of Gir lions as a group is the variability of the third lower premolar. This variation appears to have escaped notice in any literature to date. In the African lion $Pm\bar{3}$ is universally present with two well-developed, distinct roots. Table VIII tabulates the condition as found in the present sample and Plates

TABLE VIII

THE CONDITION OF Pm$\overline{3}$ IN LIONS OF THE 1963 GIR 'FIND'

Museum & No.	Condition of Permanent Lower Third Premolar					
	Left			Right		
	2 roots	fused	absent	2 roots	fused	absent
BNHS 1254		75%			100%	
BNHS 1255			X			X
BNHS 1261	no left ramus				25%	
BNHS 1267	no mandible					
BNHS 1268	no mandible					
BNHS 1291		100%			100%	
BNHS 1292		100%		?	(tooth broken and abnormal—perhaps slight fusion)	
BNHS 1293	X			X		
BNHS 1329		100%		X		
BNHS 1353		90%			90%	
BNHS 1363		50%		no right ramus		
BNHS 1364			X			X
BNHS 1389			X			X
BNHS 1391		100%			100%	
BNHS 1392			X			X
BNHS 1393	no left ramus				90%	
BNHS 1396		100%			100%	
BNHS ——	X			X		
BNHS ——	deciduous teeth being replaced by permanent					
BHHS ——		90%			90%	

NOTE. X = as per column heading

II-III show X-rays of mandibles in which this tooth is lacking. The latter is interpreted as a demonstration that the apparent absence of this tooth is not due simply to a failure to erupt. In one specimen (BNHS 1364) the deciduous alveoli of one side are clearly present but there is no trace of a permanent replacement tooth. Furthermore, in all cases where Pm$\overline{3}$ is absent, the diastema created by the missing tooth appears porous with surface irregularities and occasionally there is tissue which appears grossly to be enamel although it is not organized into anything resembling a tooth. Tentatively, it is concluded that the deciduous Pm$\overline{3}$ is present and that no replacement tooth is produced. Twelve of the earlier specimens (American Museum of Natural History, 2 ; Bombay Natural History Society, 3 ; Chicago Museum of Natural History, 1 ; British Museum, 6) have this tooth bilaterally, while in three others (British Museum) there is unilateral reduction to a rudiment. The earliest of these latter is *c.* 1910, the other two prior to 1931. Unfortunately the